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Tools for increasing visual encounter probabilities for invasive species removal: a case study of brown treesnakes

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Abstract

Early detection and rapid response (EDRR) are essential to identifying and decisively responding to the introduction or spread of an invasive species, thus avoiding population establishment and improving the probability of achieving eradication. However, detection can be challenging at the onset of a species invasion as low population densities can reduce the likelihood of detection and conceal the true extent of the situation until the species is well established. This is doubly challenging if the invading species displays cryptic behavior or is nocturnal, thus further limiting opportunities for its discovery. Survey methods that maximize a searcher's ability to detect an incipient population are therefore critical for successful EDRR. Brown treesnakes (*Boiga irregularis*) on Guåhan are a classic cautionary example of the dangers of not detecting an invasion early on, and the risk of their introduction to other islands within the Marianas, Hawai'i and beyond remains. Nocturnal visual surveys are known to detect brown treesnakes of all sizes and are the primary detection tool used by the Brown Treesnake Rapid Response Team, but detection

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probability remains low in complex forest habitats. As such, we investigated the use of two potential enhancements to nocturnal visual surveys – a live mouse lure and spray scent attractant – that may create hotspots of increased detection probability during surveys. We found that, while brown treesnake detection probabilities were low for all surveys, visual surveys conducted on transects with live mouse lures resulted in detection probabilities that were 1.3 times higher than on transects without live mouse lures. Conversely, the spray scent attractant did not increase the probability of detecting brown treesnakes compared to transects without scent, and in fact had detection probabilities that were 0.66 times lower, though the reasons for this phenomenon are unclear. Unlike scent attractants, live mouse lures likely provide both visual and olfactory cues that attract brown treesnakes to transects and thus provide more opportunities to detect and capture them. These enhancements were trialed on Guåhan, where prey populations are depressed. It remains unclear whether live mouse lures will be as effective for EDRR applications in prey-rich settings.

Keywords
Detection probability, early detection, Guam, lure, rapid response, spatial capture-recapture

Introduction

In invasive species management, the ability to quickly detect and decisively respond to the introduction or spread of an invasive species is often cited as key to the efficacy and success of eradication (i.e., early detection and rapid response or EDRR; National Invasive Species Council 2003, Hulme 2006). This can be challenging at the onset of a species invasion as low population densities can reduce the likelihood of detection and conceal the true extent of the situation until the invasive species has become established (Yackel Adams et al. 2018). Species that display cryptic behaviors and are nocturnal exacerbate this challenge, thus further limiting opportunities for their incidental discovery. Survey methods that maximize a searcher's ability to detect an incipient population are thus critical for successful EDRR. These methods may include those that supplement direct observations of the species of interest (e.g., eDNA; Dejean et al. 2012) or use attractants that draw in target species (Flaherty et al. 2018), all in the pursuit of creating and deploying an optimal suite of tools for conducting EDRR (Morisette et al. 2019; reviewed in Larson et al. 2020). However, unless field testing is undertaken well in advance of the need to deploy such methods, an emergency response may be delayed and potentially ineffective.

The brown treesnake (*Boiga irregularis*) provides a classic example of the dangers posed by a species characterized by a low detection probability that, in combination with belated concern, resulted in a delayed response to its establishment on Guåhan (in the CHamoru language, known in English as Guam) (Rodda et al. 1992). Brown treesnakes were accidentally introduced to Guåhan in the late 1940s, where they proceeded to decimate the native vertebrate fauna over the next several decades (Savidge 1987; Rodda and Savidge 2007). Now, with much of Guåhan's native vertebrate species either declining, locally extirpated, or extinct, a primary objective of brown treesnake management is to prevent the spread of the snake to other islands (Engeman

et al. 2018). Due to cultural, recreational, and military pathways of movement and cargo shipments between Guåhan and islands in the Commonwealth of the Northern Marianas (CNMI), Hawai'i, and beyond, there is an ever-present risk of the accidental spread of snakes (Engeman et al. 2018). Cargo inspections and other interdiction efforts were implemented in 1993 (Vice et al. 2005; Perry and Vice 2009) and continue today (Office of Insular Affairs/U.S. Department of the Interior 2020) with success in reducing the spread of snakes (Vice and Vice 2004). Despite efforts, by 2007, there were more than 100 reports of individual brown treesnakes (confirmed and unconfirmed) found on 3 continents and multiple oceanic islands that are thought to have originated on Guåhan (Stanford and Rodda 2007).

To respond to these reports, the U.S. Geological Survey (USGS) created the Brown Treesnake Rapid Response Team (RRT) in 2002. Among its responsibilities, the RRT is an inter-agency and inter-governmental body that serves as an on-call reporting and response service for snake sightings and provides training on the recognition and handling of brown treesnakes to people across the region (Stanford and Rodda 2007). The RRT Coordinator is tasked with establishing the credibility of all reported sightings and, if credibility is established, deploying a team to the location to initiate a search for any individuals. The primary detection tool used by the RRT is nocturnal visual surveys, as that tool has proven more effective in catching snakes of all sizes as compared to any of the available passive (e.g., trapping) methods of detection and capture (Christy et al. 2010). The effectiveness of the RRT was illustrated in October 2020, when they detected brown treesnakes on deployment to the previously snake-free island of Islan Dåno' (known in English as Cocos Island), just south of Guåhan, thereby mobilizing an ongoing EDRR effort (U.S. Geological Survey, 2020). No other incipient populations of brown treesnakes have ever been detected outside of Islan Dåno', due in a large part to the interdiction efforts and the work of the RRT (Yackel Adams et al. 2018, Yackel Adams et al. 2021).

Though visual surveys can be effective in detecting individuals, detection probabilities of brown treesnakes tend to be quite low overall, due to the snakes' use of complex habitat, cryptic behavior and coloration, and nocturnal activity patterns. While direct comparison is challenging as effort level is not easily translatable between methods, detection probabilities of $\hat{p} < 0.15$ (i.e., probability that an individual snake in the effective survey area is encountered on a given night) have been reported for typical surveys using both searching and trapping methods (Christy et al. 2010, Tyrrell et al. 2009). Consequently, a substantial amount of effort is required to infer the absence of an incipient population (Yackel Adams et al. 2018). Therefore, any method that can increase searchers' ability to encounter brown treesnakes would be highly valuable to future rapid response efforts.

As a potential tool to maximize detection probabilities during visual surveys, we investigated the use of two potential attractants for use in EDRR: 1) snake traps that contain a protected live mouse lure and 2) a scented spray applied to surveyed transects. Mouse lures can be detected by brown treesnakes from up to 20 m away (Klug et al. 2015), meaning this attractant, by providing both an olfactory and visual cue, may

create hotspots for snake detections in the area surrounding traps. Similarly, other olfactory attractants applied to a transect may also entice and create a "path" for snakes to follow and concentrate around surveyed transects. Solely relying on traps on transects to capture snakes may not be effective (Yackel Adams 2018); for example, Amburgey et al. (2021) obtained 255 camera trap photos of snakes (not necessarily unique individuals) in the vicinity of traps over 45 days, but only 5 snakes were captured in traps. Pairing live mouse lures or spray applications with visual searches may help increase the probability of detecting and capturing a snake, which is especially important in an EDRR context where finding and removing all snakes on the landscape is critical.

Methods and materials

We conducted two field experiments within the Closed Population (CP), a 5-ha (50,000 m^2) fenced area on Andersen Air Force Base in the north of Guåhan. The fence, consisting of a 1.5-m tall, galvanized mesh and chain link wall, had a bulge on both sides about 1.2 m above ground level that eliminated immigration and emigration of snakes in the study area. This fence was also bounded by a 0.5-m concrete footer and vegetation was removed 2 m to either side of the fence to provide a study population of brown treesnakes for investigation of management and population estimation methodologies (Tyrrell et al. 2009, Christy et al. 2010). This area predominantly occurred on coralline limestone with a mix of native and introduced tree species with a canopy height of 5 to 15 m. The composition of trees, shrubs, and herbaceous vines in this area was representative of much of the historically disturbed landscape of the island (Stone 1970). Within the CP were 27 parallel transects cut through the vegetation and spaced 8 m apart. A georeferenced grid cell marker was located every 16 m along each transect, creating a study area of 27 × 13 grid cells (or 351 transect points). This design allowed visual searches to be done on transects with and without experimental treatments in addition to allowing observers to assign snakes to a georeferenced grid cell when captured.

Teams of two observers conducted night-time surveys. Snakes in the CP were part of an ongoing, multi-year (starting in 2004) capture-mark-recapture (CMR) study using unique ventral scale clip patterns and internal passive integrated transponder (PIT) tags. When searchers found a snake, they attempted to scan it without handling to avoid disturbing the individual. If a PIT tag could not be remotely scanned, searchers captured snakes and further checked for a mark or PIT tag or gave a unique mark and PIT tag to previously unmarked animals. In traditional CMR, searchers avoid disturbing traps to avoid deterring animals from being captured; however, as many animals were already marked in the CP and the objective of these surveys was to test the efficacy of EDRR tools, searchers instead focused on checking these areas for snakes.

Because all data were analyzed using a framework that assumes demographic closure of the population (i.e., no immigration, emigration, births, or deaths), we truncated the data for both projects to a two-month timespan. During this two-month period, while demographic closure cannot be guaranteed, there was a low probability

of new individuals entering (i.e., being born into or found for the first time) the surveyed population or existing individuals dying. The CP was closed to emigration and immigration due to the two-way barrier surrounding the entire study area.

Live mouse lure

Searchers conducted 25 surveys between February 1 and March 31, 2015. During these surveys, transects either had no traps or live mouse lures (henceforth, no lures) placed on them or had snake traps with live mouse lures (henceforth, lures) placed at all 13 grid-cell markers on a transect. Eleven to 13 transects were surveyed every evening with four to five of these transects having lures. Lures were rotated to new locations every one to three weeks (Fig. 1A). For this design, every other transect (14 total) never had lures placed on them. The other 13 transects alternated between having lures or not depending on the rotation schedule (hence, sometimes these transects were part of the "no lure" treatment and sometimes part of the "lure" treatment). If a snake was captured inside a trap and found during a survey, it was scanned and released by searchers that same night. However, we limited our analysis to snakes found visually by searchers.

Sprayed scent

Searchers conducted 32 surveys between November 1 and December 30, 2016. During these surveys, transects were either unsprayed (henceforth, no scent) or sprayed either in the early evening before the night-time survey (fresh scent) or the previous day (old scent). We distinguished these latter two groups from each other to account for a potential lingering effect of scent. The scent consisted of a mixture of 500 ml fish fertilizer (Alaska Fish Fertilizer) and 14.74 L of water and was sprayed along the entire length of a transect on the ground (1–1.5 feet above the surface) over the course of four minutes to ensure a consistent application rate. The mixture was emitted in a flat, constant spray that resulted in little drift and even application, requiring a little under 14.74 L for three transects-worth. This scent mixture was selected from a pilot study that also tested beef blood and canned tuna mixtures (B. Lardner & A. Knox, *pers. comm.*), with the fish fertilizer eliciting the highest level of brown treesnake activity (as quantified by number of times animals entered and investigated an area with the scent applied). Brown treesnakes are scavengers that will consume a variety of carrion (Savidge 1988), and all the scents tested were readily accessible on island or easily shippable.

On most evenings of the study, nine transects were sprayed with scent and continued to be sprayed daily for three days in a row. The other 18 transects were surveyed but no spraying occurred. On the fourth day, no new spraying occurred but all transects were surveyed. After this 4-day surveying bout, a three-day break occurred after which nine new transects were sprayed (Fig. 1B). On two occasions, spraying was not completed (e.g., due to heavy rain) and only partial surveys were conducted. All transects were eventually sprayed across the study period, with each transect being part of at least three different spraying bouts.

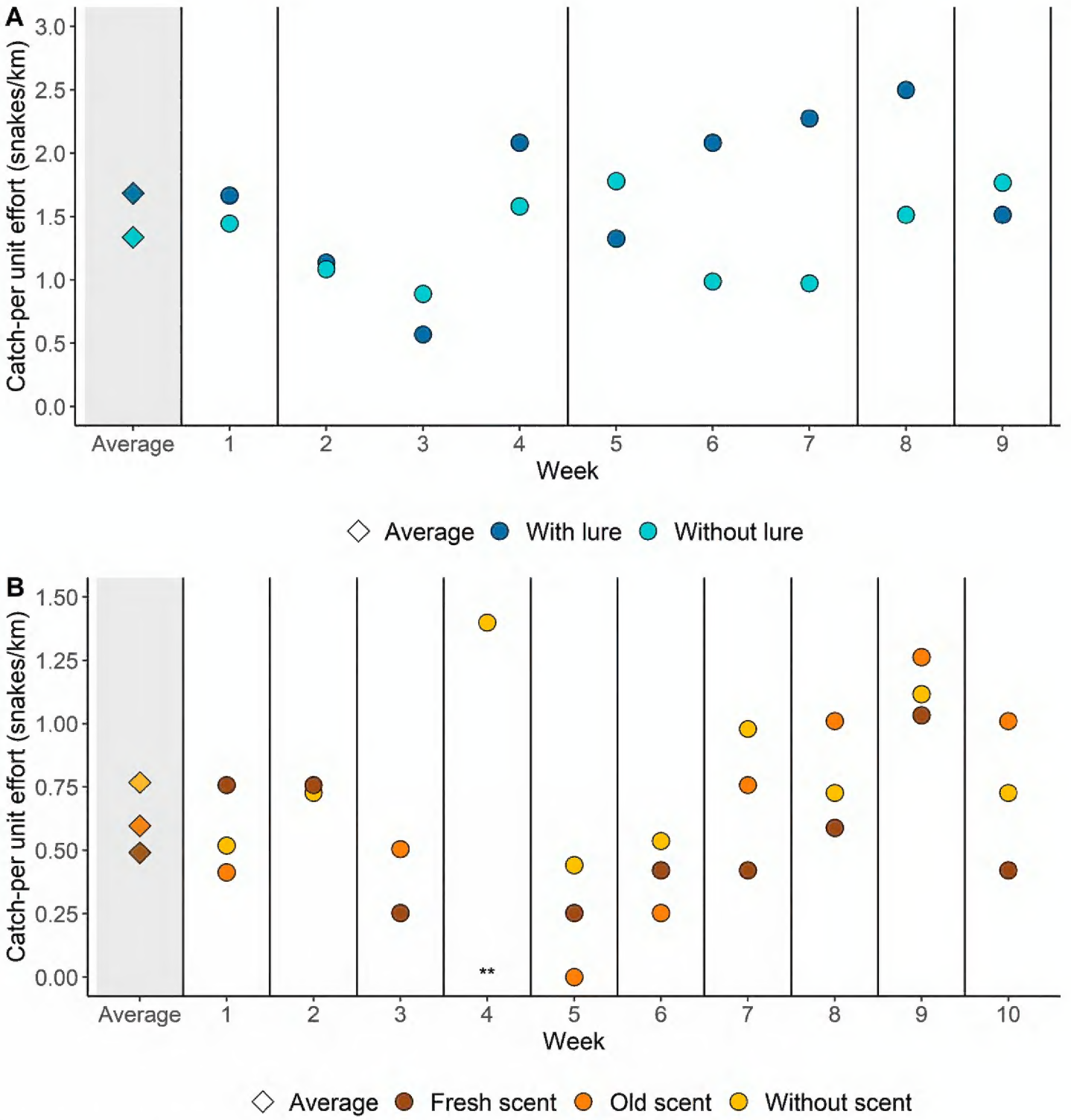

Figure 1. Weekly catch per unit effort (CPUE) of brown treesnakes along transects **A** without and with traps with mouse lures and **B** without scent, with fresh scent (applied that day), or with old scent (applied the day before). **A** Overall, average CPUE of snakes was 32% higher along transects with mouse lures than transects without such lures. Vertical lines group traps deployed at similar locations (Week 1 and 8, Week 2–4 and 9, and Weeks 5–7 denote same trap locations). **B** Overall, average CPUE of snakes was 45% and 12% higher along transects that were not sprayed as compared to those with fresh scent and old scent respectively. Asterisks indicate that no spraying occurred in week 4.

Analysis

We calculated weekly catch per unit effort (CPUE) for each project, measured as the total number of snakes caught divided by the total transect distance (km) walked during surveys each week. This metric is a commonly reported way of capturing the benefit to cost (in time) ratio of an action. We calculated this at the temporal scale of a week

to better match the time frame that treatments were implemented on a transect before being rotated to a new location and to also summarize if there were any accumulated benefits to using these treatments. However, CPUE does not lend itself to statistical testing of differences, requiring further analysis of capture data.

We also analyzed the individual capture data using a spatially explicit capture mark-recapture (SCR or SECR) model (Royle et al. 2014) in a Bayesian framework. This model allows for the estimation of population abundance and density within the state space (*S*; here, the dimensions of the CP) by relating encounters of marked individuals to specific spatial locations across time, e.g., marked individual *i* at each grid cell *j* and occasion *k* (y_{ijk}). While we were not focused on estimating abundance or density, this model allowed us to estimate the detection probability for snakes on the landscape. The process model assumes there is some activity center (*s*) around which each animal in the study area uses space. As an animal moves around the landscape, its probability of being detected at a grid cell is a function of the distance between its activity center *s* and grid cell *j* and two parameters describing the encounter rate. The first parameter describes the decline in encounter probability as the distance between the grid cell and its activity center increases (σ), and the second is a baseline encounter rate at a distance of zero (i.e., λ_0, the probability that an individual lives in the grid cell in which it was caught that night).

We ran one model for each project where we allowed the baseline encounter rate ($\lambda_{STATUS_{jk}}$) to vary by the lure or scent of each grid cell *j* at the time *k*. For both analyses, we assumed a half-normal detection function such that

$$\lambda_{ijk} = z_i \lambda_{STATUS_{jk}} e^{\left(\frac{-\|s_i - x_j\|^2}{2\sigma^2}\right)} \quad (1)$$

where $||s_i - x_j||$ is the squared Euclidean distance between each activity center (s_i) and grid cell (x_j). For the first analysis, the status of a grid cell could take three forms: 1) inactive (i.e., not surveyed that evening), 2) active and without a lure (λ_{nolure}), or 3) active and with a lure (λ_{lure}). For the second analysis, the status of a grid cell could take four forms: 1) inactive, 2) active and without scent ($\lambda_{noscent}$), 3) active and with fresh scent ($\lambda_{freshscent}$), or 4) active and with old scent ($\lambda_{oldscent}$).

We used a data augmentation approach to estimate the number of individuals present in the study area but not detected during the study (Royle et al. 2014). A latent indicator variable, z_i, denotes the probability that an individual is part of the population (1) or not (0). We assumed $z_i \sim Bernoulli(\psi)$ for $i = 1, 2, \ldots, M$ individuals where *M* is a value much larger than the expected abundance. The latent indicator variable z_i limits encounters to those individuals that are part of the population, and abundance is then simply the sum of all instances where $z_i = 1$.

We fit both models using a data augmentation value of $M = 250$ and vague priors where $s_i \sim Uniform[S]$, $\lambda_{STATUS} \sim Uniform(0,1)$, $\psi \sim Uniform(0,1)$, and $\sigma \sim Uniform(0,50)$.

We ran all models using three parallel chains comprised of 1,000 adaptation iterations followed by 2,000 iterations and no burn-in or thinning. Model convergence was determined by visual inspection of traceplots and Gelman Rubin statistics ($\hat{R} \leq 1.01$; Gelman et al. 2013). Example code used to fit these models is provided in Suppl. material 1 (R code to fit the spatial capture-recapture model in JAGS).

We also calculated the probability (% of total Markov chain Monte Carlo iterations) per project that the encounter probability when using each attractant was greater or less than the encounter probability without the use of that attractant. We also calculated the mean difference between the encounter probabilities (e.g., $\lambda_{lure} - \lambda_{nolure}$).

Prediction

Using values estimated from the data that impact the way searchers detect snakes (λ_{STATUS} and σ), we simulated data to better understand the way each attractant could impact the probability of detecting snakes on a given night. For a single snake with an activity center s in the very center of the study area, we simulated a single evening survey where the entire study area (the same dimensions of CP; 50,000 m^2) was uniformly subjected to each of the different attractants or not (e.g., every grid cell contained a lure or not). We estimated the encounter probability at each grid cell in the study area and calculated the probability that the individual would be detected at least once in the study area when using that attractant (or lack thereof). We fit all models in JAGS (Plummer 2003) via the jagsUI package (Kellner 2018) in R (R Core Team 2019). Simulation code is provided in Suppl. material 2.

Results

Live mouse lure

During this study, we captured 100 unique individuals, with snakes being caught an average of 1.9 times (range: 1–5 times) and 3–14 snakes being caught every evening. The mean snout-vent length (SVL) of captured snakes was 918.91 mm (min = 566, max = 1205). Weekly CPUE was often higher on transects with live-mouse lures present (Fig. 1A; 0.56–2.50 snakes/km with lures as compared to 0.89–1.78 snakes/km without lures), with CPUE 32% higher on average on transects with lures as compared to those without.

Encounter probabilities of snakes in grid cells with lures was generally higher ($\lambda_{lure} = 4.26e^{-3}$ [95% credible interval {CI} = $2.98e^{-3}$, $5.82e^{-3}$]) than those in grid cells without lures ($\lambda_{nolure} = 3.25e^{-}3$ [$2.33e^{-3}$, $4.37e^{-3}$]), though 95% CIs overlapped (Fig. 2A). However, there was a 97% probability that $\lambda_{lure} > \lambda_{nolure}$, and the difference between λ_{lure} and λ_{nolure} was 0.001 ($-1.11e^{-4}$, $2.23e^{-3}$). We estimated the scale parameter, σ, to be 32.29 m (28.57, 36.53). We estimated a mean abundance of 134.31 (118, 154) snakes and a density of 27 (24, 31) snakes per ha.

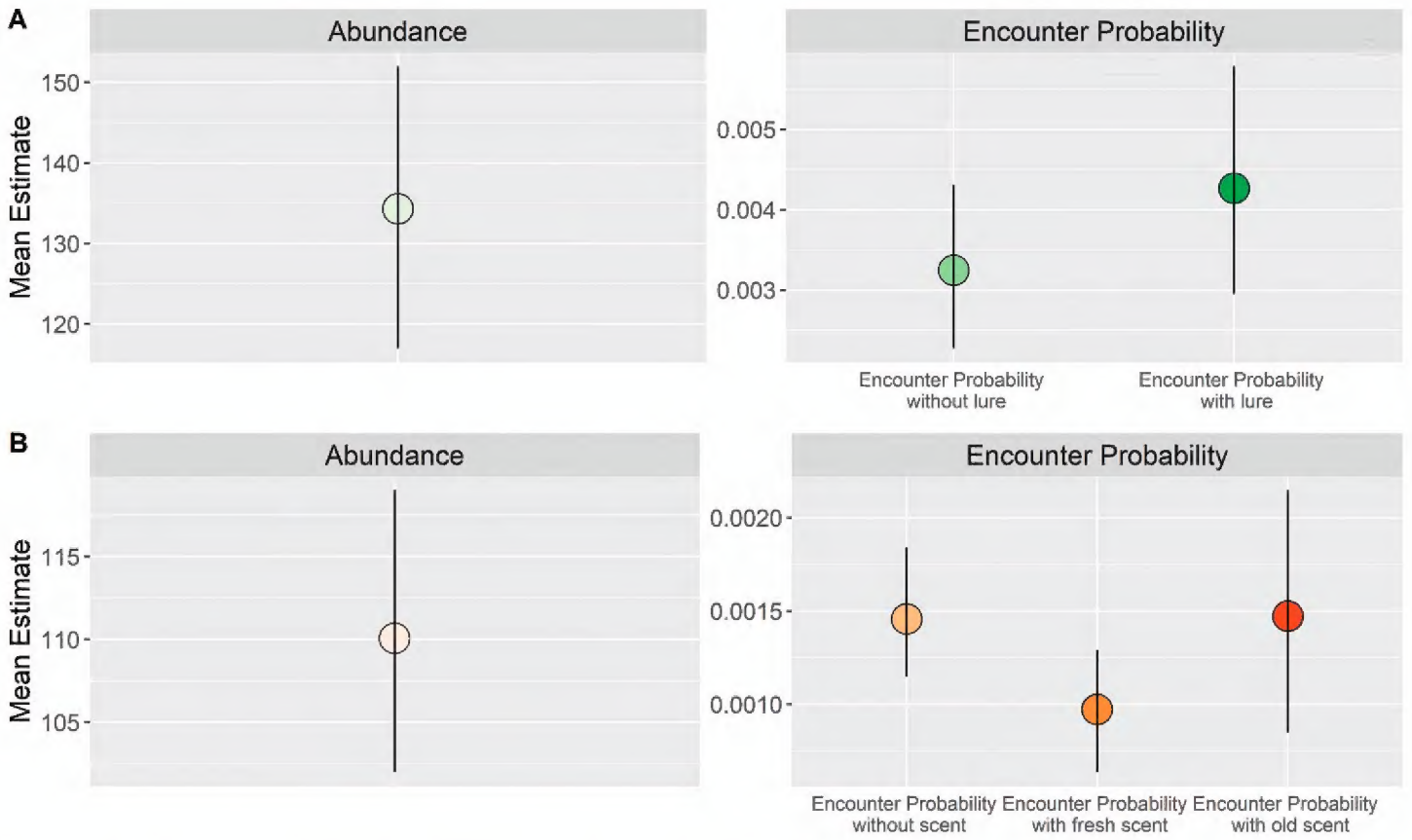

Figure 2. Mean estimated abundance (left panels) and encounter probabilities for visual surveys (right panels) on transects **A** without and with lures and **B** with different scent treatments. Lines around point estimates represent 95% credible intervals. Note that y axes are different.

Sprayed scent

In this study, we captured 96 unique individuals, with snakes being caught an average of 2.5 times (range: 1–8 times) and 2–18 snakes being caught every evening. The mean SVL of captured snakes was 950.21 mm (min = 462, max = 1203.75). Weekly CPUE was highest on transects without any scent sprayed (Fig. 1B; 0.44–1.40 snakes/km without scent as compared to 0.25–1.03 snakes/km with scent), with CPUE 45% higher than on transects with fresh scent and 12% higher than on those with old scent.

Encounter probabilities of snakes on transects that were unsprayed ($\lambda_{noscent} = 1.46e^{-3}$ [$1.14e^{-3}$, $1.83e^{-3}$]) or sprayed the day before ($\lambda_{oldscent} = 1.47e^{-3}$ [$1.14e^{-3}$, $1.83e^{-3}$]) were higher than for snakes on transects with fresh scent ($\lambda_{freshscent} = 0.97e^{-3}$ [$0.67e^{-3}$, $1.33e^{-3}$]), though again 95% CIs overlapped (Fig. 2B). During visual surveys with no scent, snakes had higher encounter probabilities than during surveys with scent, where there was a 99% and 50% probability that $\lambda_{noscent} > \lambda_{freshscent}$ and $\lambda_{noscent} > \lambda_{oldscent}$ respectively. In this case, the difference between $\lambda_{noscent}$ and $\lambda_{freshscent}$ was $4.76e^{-4}$ ($9.98e^{-5}$, $8.65e^{-4}$) and $\lambda_{noscent}$ and $\lambda_{oldscent}$ was $1.19e^{-6}$ ($-6.83e^{-4}$, $5.91e^{-4}$). Additionally, snakes on transects with older scent had a higher encounter probability than those on transects with freshly sprayed scent, with a 94% probability that $\lambda_{oldscent} > \lambda_{freshscent}$. The difference between $\lambda_{oldscent}$ and $\lambda_{freshscent}$ was $4.75e^{-4}$ ($-1.38e^{-4}$, $1.19e^{-3}$). The estimated scale parameter, σ, was slightly higher than in the lure study at 40.95 m (36.88, 45.51) and the mean estimated abundance was slightly lower at 110.07 (102, 120) snakes and a density of 22 (20, 24) snakes per ha.

Prediction

Using the estimates from the live-mouse lure component, we found that the probability of detecting a single individual on a single night (when searching every grid cell) in a study area entirely lacking a lure was 0.66 (0.55, 0.77) but increased to 0.76 (0.64, 0.86) with lures placed at every grid cell. Using estimates from the sprayed scent project, we found that the probability of detecting a single individual on a single night (when searching every grid cell) in a study area entirely lacking scent or with older scent was 0.39 (0.32, 0.47) or 0.39 (0.26, 0.53), respectively. The lowest probability of detection, 0.28 (0.21, 0.37), was in a study area with fresh scent.

Discussion

For EDRR, the probability of detecting an incipient population dictates how rapid a management response can be assessed and implemented. We tested the utility of pairing visual surveys with attractants (i.e., lures and scent) to increase the probability that searchers would encounter brown treesnakes during a rapid response effort. The CI of estimates overlapped likely due to imprecision caused by small sample sizes and limited recaptures (Fig. 2); however, our raw capture rates scaled by effort (CPUE; Fig. 1), the probabilities of having increased encounter probabilities, and the differences between encounter probabilities indicated increased snake captures on transects using live-mouse lures as attractants but not on those using spray attractants. We show that this can manifest itself in gains in the probability of detecting a snake on the landscape, with a 15% increase in the probability of detection. However, using freshly sprayed scent on transects resulted in the lowest probability of detection on a given night, decreasing the probability of detection of a snake by 28%.

When considering the efficacy of different attractants, a live-mouse lure provides both an olfactory and visual cue to brown treesnakes (Shivik 1998, though see Shivik and Clark 1997), potentially attracting snakes to, and then keeping them on, transects long enough for searchers to encounter them. On camera traps, snakes stayed in the field of view with live mouse lures for an average of 11 minutes but up to an hour in many cases and often appeared to leave and return to the lure multiple times (Amburgey et al. 2021). As such, even though a pilot study showed brown treesnakes were interested in the fish fertilizer scent, the lack of a prey item to retain attention (Lindberg et al. 2000) may result in the benefits of this attractant being highly ephemeral. Work on brown treesnakes has also shown that lipids are one of the primary components of scent attraction (Kimball et al. 2016), and fish fertilizer likely has less lipids in it than other possible attractants. Additionally, visual detection of brown treesnakes is challenging in the forests of Guåhan. For example, Savidge et al. 2011 explains how imperfect detection by human observers, even when partnered with canine detector dogs, can lead to a low number of snake captures. With scent spread out evenly across a transect and on multiple transects, searchers may not have a concentrated hotspot (i.e., a trap)

upon which to focus their search or may actually deter predators with an unrewarding and confusing signal (Norbury et al. 2021), limiting the utility of this attractant.

Our estimated abundances and densities for both projects are consistent with other studies on this population (Tyrrell et al. 2009, Christy et al. 2010, Amburgey et al. 2021) in addition to the densities of snakes in forested landscapes of Guåhan (Rodda et al. 1999), indicating that encounter rates in these studies would be comparable to those in established populations of brown treesnakes. This highlights the challenge of EDRR in the case of an incipient population of brown treesnakes, as individual encounter probabilities were low ($\lambda < 5.0e^{-3}$) and effort was substantial to capture a minimal number of animals even at this high population density (Fig. 1). In our predictive simulation, substantial effort (i.e., every grid cell being surveyed in a single night) was required to achieve higher detection probabilities. Population density was slightly lower during the scent experiment and sampling occurred during the wet season, potentially explaining the overall lower encounter probabilities as compared to the lure experiment. It is also important to note that, in this study, model estimates represent survey-specific encounter probabilities while CPUE was summed over each week, potentially showing that the benefits of using attractants during EDRR may take time (or space, as shown by our predictive simulation) to accrue. For a given survey, using a lure may not drastically alter the probability of encountering a snake on a given evening; however, over time or over space, the benefits of using a lure may accumulate. Marginally higher encounter probabilities on transects with lures may potentially manifest as a benefit when multiple surveys are conducted. With such low encounter probabilities, any improvement would be beneficial. Additionally, the fact that searchers rotated lures means that there may have been some delay in the response of snakes as they must be attracted from the surrounding landscape, and there should be additional investigation of whether it is beneficial to establish permanent locations (as a reliable attractant) or rotate locations (in order to intersect more potential areas of snake use). Fed snakes also remain inactive for several days post meal consumption (Siers et al., 2018), meaning some proportion of the population will not be available for detection on a given evening and surveys should be done for long enough to ensure there are sufficient detection opportunities.

In a novel environment with high prey densities, a snake's activity status would more often be in a "fed" vs. "foraging" state and the efficacy of a lure could be limited due to an abundance of alternate prey options (Gragg et al., 2007). Snake-free islands in this region have higher prey densities as compared to Guåhan (Wiewel et al., 2009, Campbell III et al., 2012), stressing the need for further investigation of this tool in experimental situations (e.g., laboratory or simulation studies) better representing newly invaded habitats. Snake movement is also influenced by the availability of prey and density of conspecifics (Christy et al. 2017), potentially changing the area that needs to be searched around a credible sighting or capture in the case of an incipient population. This can be challenging in environments with dense forest and lack of standardized survey locations, potentially requiring the establishment of survey transects on these landscapes. Additionally, certain smaller-sized snakes may be refractory to detec-

tion and removal (Vice and Vice 2004) thus increasing the probability of them being transported to other islands. These smaller snakes are less interested in mouse lures due to size-specific shifts in predation during the brown treesnake life cycle (Lardner et al. 2009), potentially limiting the utility of these lures. However, in the case of an invasive species, such as the brown treesnake, which has caused ecological collapse and resulted in massive economic repercussions through reduced tourism, infrastructure damage, and continued interdiction and suppression efforts (Rodda and Savidge 2007), any tools that can potentially help maximize the detection of an incipient population or boost capture rates during a rapid response may be worth implementing.

Conclusion

Previous work in EDRR has highlighted the use of supplemental data types and attractants as a means to ensure detection of incipient populations that can cause massive, ecosystem-wide damage (Dejean et al. 2012; Flaherty et al. 2018; Larson et al. 2020 and resources therein). Use of attractants in a rapid response would require an explicit discussion of the direct management benefit obtained with respect to the potential costs (including obstacles of availability and quarantine procedures in the case of live animals) of deploying that method. Mouse lures may be costlier to place and maintain than a scented spray but appear to be more effective at increasing detection of snakes along surveyed transects. While the mean encounter probability on transects with mouse lures was still small, as snake traps with mouse lures are already in use at ports and airports in the region, it may be that pairing visual searches with mouse lures (inside of traps or in a different format) can provide searchers an edge while performing a rapid response. Additionally, having traps on the landscape represents a continuous opportunity to capture snakes, an additional benefit to weigh when selecting strategies to deploy. It is necessary for managers to explicitly consider the costs of deploying and maintaining traps and transects with regards to the potential gains when selecting a strategy.

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or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All code and data to run these analyses are available at https://github.com/amburgey/Browntreesnake_ATTRACTANTS.

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Supplementary material 1

R code to fit the spatial capture-recapture model in JAGS

Authors: S.M. Amburgey, A.A. Yackel Adams, B. Gardner, B. Lardner, A.J. Knox, S.J. Converse

Data type: model code

Explanation note: R code to fit the spatial capture-recapture model in JAGS. Code example is for the mouse lure project but was similar to that used for the spray scent project. Simulated data are included for reference as to the structure and form of data input into the model.

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Supplementary material 2

Code used to simulate detection probabilities

Authors: S.M. Amburgey, A.A. Yackel Adams, B. Gardner, B. Lardner, A.J. Knox, S.J. Converse

Data type: model code

Explanation note: Code used to simulate detection probabilities and observations of a single snake in the study area based on estimated parameters (from JAGS model, saved as "out"). Example code shows calculations for mouse lure predictions but is similar to that used for spray scent predictions. By using all the samples in the posterior, we estimated uncertainty.

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